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AFFERENT PROJECTIONS OF THE CLARE-BISHOP AREA IN THE CAT CORTEX: A HORSERADISH PEROXIDASE STUDY[1]

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ABSTRACT. Recent studies of the Clare-Bishop (CB) area (the lateral suprasylvian area) have supported the role of this extrastriate, retinotopically-organized cortical region in visual and oculomotor functions. Anatomical studies were undertaken using retrograde horseradish peroxidase (HRP) techniques to define its afferent connections. Results indicate that CB receives substantial input from the ipsilateral striate and parastriate visual cortex (areas 17, 18 and 19), the contralateral CB area, claustrum, thalamus (ventral anterior nucleus, intralaminar nuclei, LP-pulvinar complex, posterior nucleus, dorsal lateral geniculate nucleus), and several brain stem nuclei (rostral linear nucleus, ventral tegmental area of Tsai, locus ceruleus, raphe nuclei). The results of the present investigation provide an anatomical substrate for the proposed role of the Clare-Bishop area in visual and oculomotor functions.

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INTRODUCTION

A cortical area in the cat that appears to be functionally interrelated with the visual cortex (areas 17, 18 and 19) was first observed in the lower one-half of the medial bank of the middle suprasylvian sulcus by Clare and Bishop (1954) in neurophysiological recording studies. This extrastriate visuotopic region of cortex, now commonly referred to as the Clare-Bishop (CB) area, is thought to be synonymous with the lateral suprasylvian (LS) area of Heath and Jones (1971). Recent electrophysiological data (Palmer, Rosenquist and Tusa 1978) have shown that the LS area responsive to visual stimulation extends beyond the limits of its original description through the full length of both the medial and lateral banks of the middle suprasylvian sulcus and caudally into the deep parts of both banks of the posterior suprasylvian sulcus. These investigators determined that LS is actually comprised of 6 mirror-symmetrical, topographically-organized representations of the visual fields, having as their axes of symmetry the fundi of the middle and posterior suprasylvian sulci.

The cortical input to this area reportedly comes from both ipsilateral and contralateral areas 17, 18 and 19 (Maciewicz 1974, Gilbert and Kelly 1975), contralateral CB area (Heath and Jones 1971, Shoumura 1972, Maciewicz 1974), as well as from the ipsilateral middle suprasylvian area and fundus of the middle and ventral portions of the coronal gyrus (Kawamura and Otani 1970).

Most of the subcortical input to the CB area appears to arise from the posterior thalamus as demonstrated by silver impregnation studies (Graybiel 1972, Hajdu et al. 1972, Jones 1974, Niimi et al. 1974), HRP investigations (Kennedy and Baleydier 1977, Berson and Graybiel, 1978; Hajdu et al. 1978) and autoradiography (Rosenquist et al. 1974, Palmer et al. 1978).

A great deal of disagreement centers around the CB area and its relationship with the dorsal lateral geniculate nucleus.

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Several studies (Narikashvili et al. 1969, Niimi and Sprague 1970, Burrows and Hayhow 1971) suggested direct projections from the major laminae (A AI and C) of dLGN to the CB areas. Others (Gilbert and Kelly 1975, Robertson 1976, Kennedy and Baleydier 1977) indicated that a direct neural pathway existed between the medial interlaminar nucleus (MIN) of dLGN and the CB area but not between the major laminae and this cortical region. Recent studies (Rosenquist et al. 1975, LeVay and Gilbert 1976, Hughes 1978) have shown a direct projection from lamina C of the dLGN to the region of the lateral suprasylvian area.

Since disagreement exists concerning the neural connections of the CB area, this study was undertaken to elucidate more clearly the major afferent projections to this cortical area by use of retrograde transport of HRP based on the modifications designed by Mesulam (1976, 1978).

METHODS AND MATERIALS

Four adult cats within a weight range of 2.0 – 3.5 kg were used in this study. A craniotomy was performed under aseptic conditions exposing the dorsolateral aspect of the brain. Solid HRP gel implants (15% HRP in polyacrylamide gel, Griffin et al. 1979) or injections of 5 μl of a 25% HRP solution, were made along the lateralmost aspect of the crown of the left middle suprasylvian gyrus with penetration through the medial wall of, and parallel to, the suprasylvian sulcus. The "slow-release" gel provided prolonged release of the HRP and helped to confine the enzyme to the injection site, limiting submeningeal and intravascular diffusion of the HRP. Survival times ranged from 24-48 h. Subsequently, the animals were perfused, following a saline wash, with 1% paraformaldehyde and 1.25% glutaraldehyde in 0.1 M phosphate buffer. Upon removal, brains were photographed, blocked, and then placed into a 10% sucrose buffer solution and refrigerated overnight. Coronal sections of 50 μm were cut using a freezing microtome and collected in a compartmentalized plastic tray containing 0.1 M phosphate buffer. Selected sections were later processed to demonstrate reaction product according to either the (BDHC) or (TMB) procedures (Mesulam 1976, 1978). The reacted HRP sections were counterstained with neutral red. The distribution of cells containing reaction product (HRP) were charted in projection drawings of appropriate sections by using light and/or darkfield microscopy. Cortical designations were based on Heath and Jones (1971) and Reinoso-Suarez (1961), and subcortical according to Rioch (1929), Snider and Niemer (1961) and Berman (1968).

LIST OF ABBREVIATIONS

A	amygdala
AC	anterior commissure
AM	anterior medial nucleus
AV	anterior ventral nucleus
B	nucleus of diagonal band (of Broca)
BDHC	benzidene dihydrochloride
BF	basal forebrain
C	cingulate cortex
CB	Clare-Bishop area
cc	crus cerebri
CL	central lateral intralaminar nucleus
CLA, cla	claustrum
CN	caudate nucleus
COR	coronal sulcus
CRU	cruciate sulcus
DLGN, dLGN	dorsal lateral geniculate nucleus
DMH	dorsomedial hypothalamus
ESCA	anterior ectosylvian sulcus
FEF	frontal eye field
HN	habenular nucleus
HRP	horseradish peroxidase
IC	internal capsule
III	oculomotor nerve
LAT	lateral sulcus
lc	locus ceruleus
LD	lateral dorsal nucleus
LH	lateral hypothalamic area
LP	lateral posterior nucleus
MD	dorsal medial nucleus
MIN	medial interlaminar nucleus of dLGN
OC	optic chiasm
OT	optic tract
P, put	putamen
PN	posterior nucleus (of Rioch)
PRS	presylvian sulcus
PS	posterior suprasylvian gyrus
PUL	pulvinar
R	reticular nucleus
RAN	anterior rhinal sulcus
RN	red nucleus
RPS	posterior rhinal sulcus
SI	primary sensory area
SPL	splenial sulcus
SUB	subthalamic nucleus
SUPS	suprasylvian sulcus
TMB	tetramethyl benzidene
VA	ventral anterior nucleus
VL	ventral lateral nucleus
VMH	ventromedial hypothalamus
VM	ventral medial nucleus
VP	ventral posterior nucleus
ZI	zona incerta

RESULTS

I. CORTICOCORTICAL PROJECTIONS

An injection or gel placement of HRP in the CB area resulted in neuronal labelling within ipsilateral areas 5, 7, 17, 18, 19, 20, 21, the cingulate gyrus, the suprasylvian fringe region and the posterior suprasylvian gyrus (of area 21).

The most rostral source of cortical afferent projections to CB was from area 5 where a few, small polymorphic shaped cells of lamina III were retrogradely-labelled within the posterior sigmoid gyrus near the lateral sulcus. More caudally, at the junction of areas 5 and 7, small labelled polymorphic and pyramidal neurons were present within laminae III–V (fig. 1B). Lamina III of the rostral suprasylvian fringe area also contained small labelled multiform cells. A more extensive gel placement labelled neurons within other frontal cortical areas including areas 6 and 8 (frontal eye field, FEF), in the deep laminae of the medial bank of the presylvian sulcus, and the primary sensory area (fig. 1A).

Many pyramidal neurons were labelled in lamina III at the junction between the rostral part of area 17 and medial part of area 19 (fig. 1F). A caudal progression through area 17 revealed a consistent pattern of labelled pyramidal neurons in lamina III (fig. 1I). A larger and more posterior HRP placement produced labeling of pyramidal neurons in lamina III and V and many small multiform cells in lamina VI of the caudal part of area 17 (fig. 1K).

The rostral part of area 18 contained heavy labelling of lamina III pyramidal cells along the crown and lateral wall of the lateral gyrus (fig. 1G). Caudally, area 18 was also observed to contain large numbers of labelled neurons. Such neurons were pyramidal in shape and found in laminae III and IV (fig. 1I and 1J).

Labelled cells of area 19, first observed within lamina III along the lateral wall of the lateral sulcus (fig. 1D), extended caudally to area 21. Other ipsilateral cortical areas projecting to CB include area 20, the posterior suprasylvian gyrus (fig. 1J) and the cingulate cortex. More extensive gel placements resulted in ipsilateral labeling of neurons in the ectosylvian and perirhinal cortices in addition to those described above.

It was demonstrated that CB received contralateral input from areas 18, 19, 21, the suprasylvian fringe region, the posterior suprasylvian gyrus and the contralateral CB area. The heaviest projection was from lamina III pyramidal neurons in the contralateral CB (fig. 1H). A few polymorphic cells of the deeper laminae also exhibited reaction product.

II. SUBCORTICAL PROJECTIONS

The CB area receives substantial projections from basal telencephalic structures (mainly the claustrum), the diencephalon, and several brain stem nuclei.

A. CLAUSTROCORTICAL–The ipsilateral claustrum contributes a remarkably heavy projection to the CB area (figs. 2A and 2B). The cells labelled by CB implants are small to medium-sized polymorphic shaped neurons that lie predominantly in the claustral intermediate zone. The number of labelled neurons within the claustrum can be correlated with the size of the HRP placement. A few labelled cells were also observed in the dorsal part of the contralateral claustrum. Large heavily labelled cells were in the ipsilateral putamen and within the external pallidal lamina (fig. 2A) whose morphology resembled those of the nucleus basalis (of Meynert). Other telencephalic areas labelled by CB implants of HRP included the nucleus of the diagonal band of Broca (fig. 1B), the basal forebrain (substantia innominata) (fig. 1C) and basal amygdaloid nucleus (pars lateralis).

B. THALAMOCORTICAL–As expected, the most significant subcortical projection to the CB area comes from the thalamus. The following thalamic nuclei apparently project to the CB area: the ventral anterior, central lateral, lateral dorsal nucleus, the LP-pulvinar complex, the posterior nucleus, the dorsal lateral geniculate nucleus

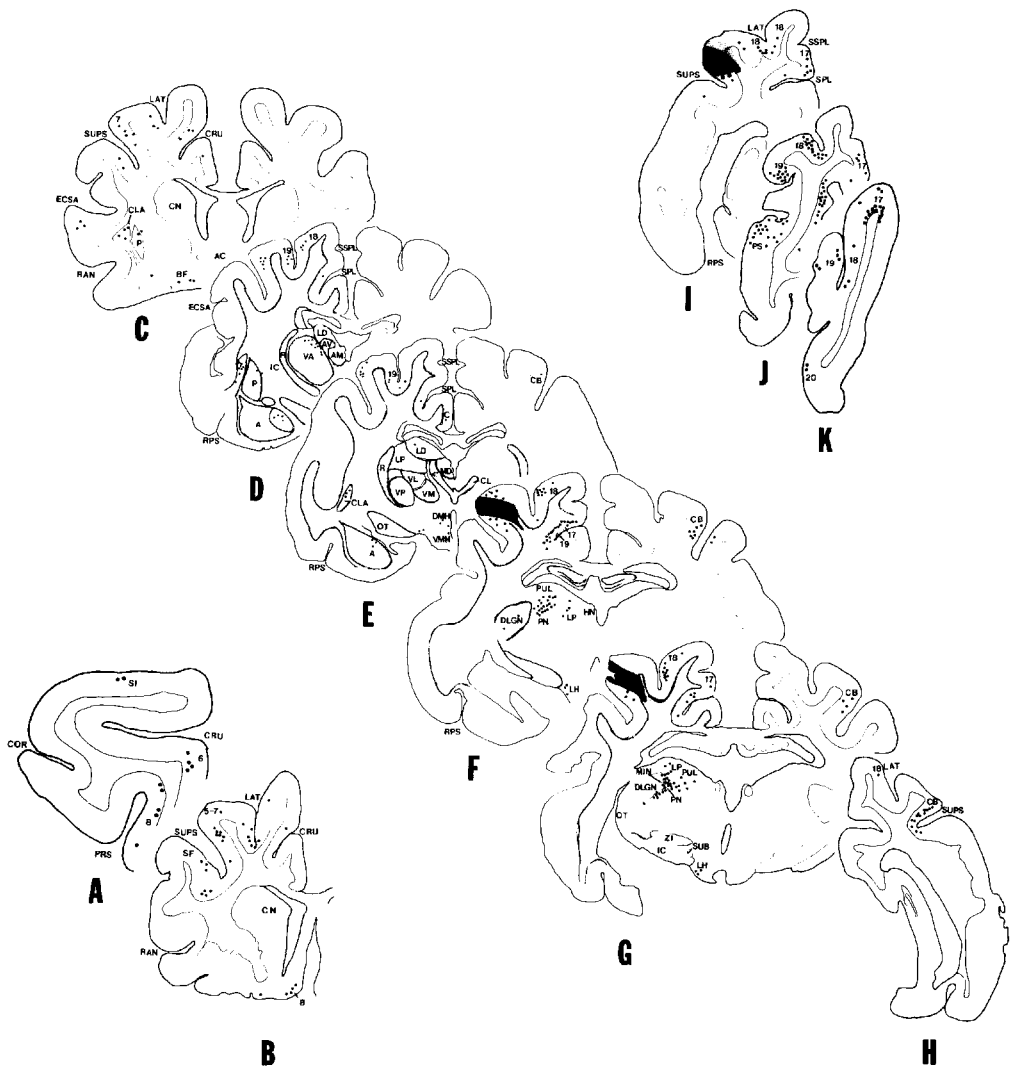

FIGURE 1: Chartings of coronal sections arranged in a rostral (A) to caudal (K) sequence. Notice HRP gel implant site in left hemisphere Sections F–I (blackened area). Black dots indicate labelled neurons in the various sections. Cortical designations are based on Heath and Jones (1971) and/or Reinoso-Suarez (1961).

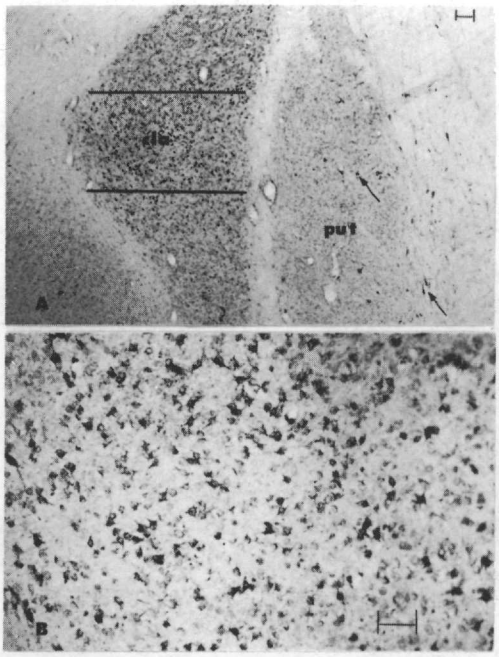

FIGURE 2: Brightfield photomicrographs showing retrogradely labelled cells in the claustrum and adjacent putamen. A. Heaviest concentration of neurons was observed in the intermediate zone (between lines) of the claustrum. Also, observe labelled neurons in putamen and external pallidal lamina (at arrows). B. Higher power view of intermediate zone of claustrum. Bar in each photograph represents 60 μm.

and the medial interlaminar nucleus (MIN) of DLGN.

The ipsilateral projection from VA is provided by small to medium-sized multiform cells located primarily in the dorsal and dorsomedial aspect of this nucleus (fig. 1D and 3A, 3B) near its border with the anterior group of thalamic nuclei. Medium-sized neurons give rise to a projection to CB from the central lateral nucleus of the intralaminar group (fig. 1E) and a slight projection from LD. A more extensive HRP placement resulted in increased labelling within these nuclear structures as well as labelling within the paracentral and central medial intralaminar nuclei.

The heaviest subcortical projection comes from the ipsilateral posterior thalamus. It was demonstrated that multiform cells throughout the rostrocaudal extent of PN project to the CB area. These cells were most conspicuous as they assumed a vertical orientation along the ventromedial border of the optic tract toward the LP-pulvinar complex (fig. 1G). In this nuclear complex, labelled cells were found in the more lateral pulvinar region dorsal to the DLGN and in both the lateral (corticorecipient zone) and medial (tectorecipient zone) subdivisions of the lateral posterior nucleus (Berson and Graybiel 1978). A more extensive HRP placement demonstrated a more pronounced demarcation at the rostral tip of DLGN between areas containing cells within the pulvinar and those in LP (fig. 4A, 4B). Here a preponderance of cells containing reaction product could be seen in both the pulvinar immediately dorsomedial to DLGN and within the so-

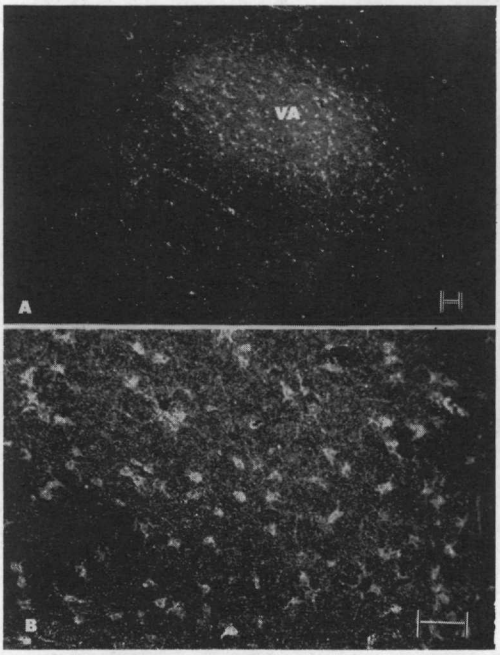

FIGURE 3: Darkfield photomicrographs showing labelled neurons in the dorsal and dorsomedial portion of the ipsilateral ventral anterior nucleus (VA). A. Low power view of VA with labelled cells (light area). B. Higher power of numerous HRP-filled neurons in VA. Bar in each photograph represents 60 μm.

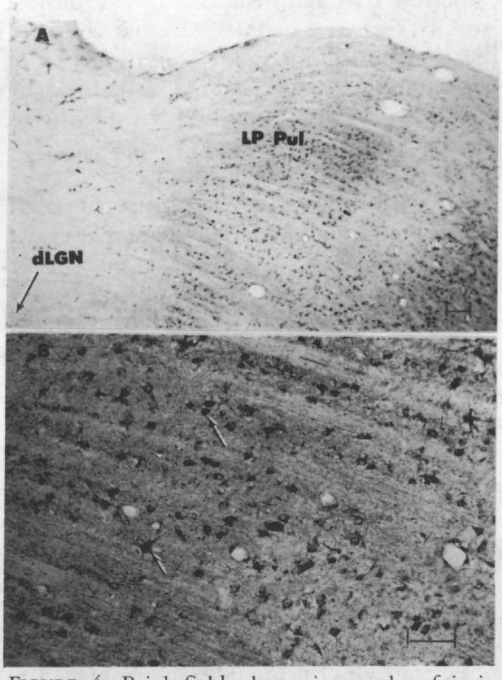

FIGURE 4: Brightfield photomicrographs of ipsilateral LP-Pulvinar complex showing distribution of labelled cells. A. Low power view of LP-Pulvinar complex showing regions containing numerous labelled cells. B. High power view of A demonstrating quite clearly the heavily labelled neurons of the posterior thalamus (at arrows). Bar in each photograph represents 60 μm.

called (Berson and Graybiel 1978) lateral intermediate nucleus. Also, labelled neurons were found between the fascicles of the optic tract and within the medial interlaminar nucleus. A mixture of small, medium and large multipolar cells project from the main laminae (A, AI and C) of DLGN to the CB area (fig. 5A, 5B).

Finally, the lateral and dorsomedial hypothalamic areas were found to project to the CB area. A small cluster of large multipolar cells was labelled in the lateral hypothalamus ventromedial to the posterior limb of the internal capsule from the middle to the caudal hypothalamus. Such neurons appeared to be continuous caudally with the cells of the rostral linear nucleus (fig. 1E-1G).

C. BRAINSTEM PROJECTIONS–The CB received afferent input from the rostral linear nucleus, the ventral tegmental area (of Tsai), the dorsal raphe nucleus, locus ceruleus (figs. 6A, 6B) and the central tegmental field. A more extensive gel placement of the HRP resulted in heavier labelling in the above nuclear structures and in addition revealed retrogradely-labelled cells in the reticulotegmental and superior central nuclei.

DISCUSSION

The results of the present study provide additional support for the suggestion that the Clare-Bishop or lateral suprasylvian area is primarily involved in visual mechanisms. This investigation showed that the CB area has connections with cortical regions and nuclear structures classically associated with visual functions, including afferent striate and parastriate cortical areas

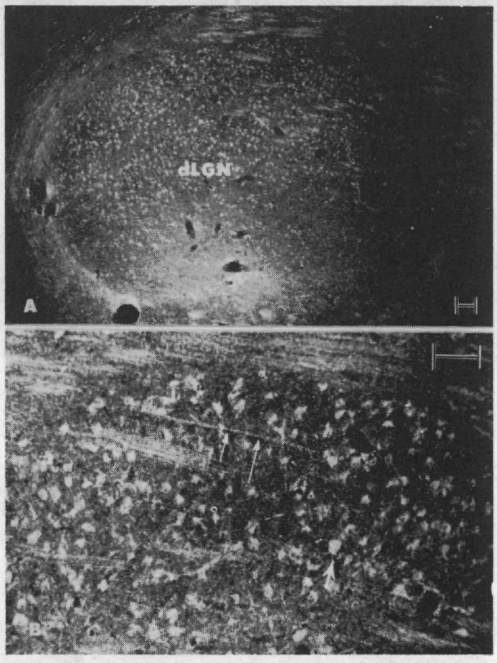

FIGURE 5: Darkfield photomicrographs of ipsilateral dorsal lateral geniculate nucleus (dLGN). A. Low power view of dLGN showing labelled cells throughout this nuclear structure. B. Higher power view of A. Note abundance of retrogradely-labelled cells and orthogradely-transported enzyme is also apparent (smaller arrows). Bar in each photograph represents 60 μm.

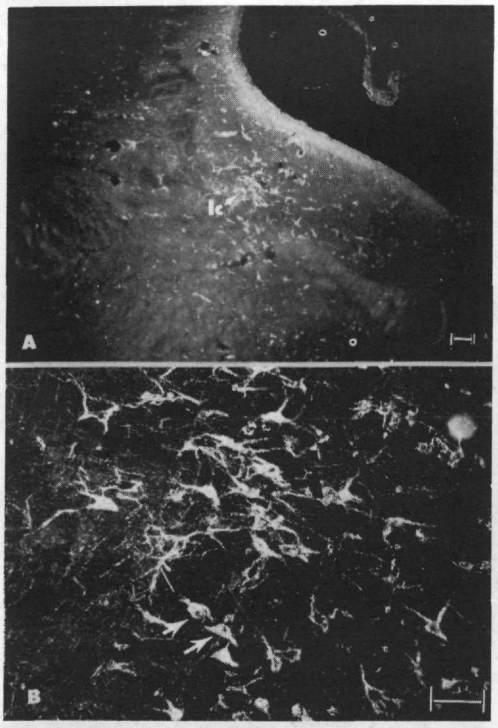

FIGURE 6: Darkfield photomicrographs of ipsilateral locus ceruleus (lc). A. Low power view of labelled cells in locus ceruleus (at arrow). B. Higher power view of locus ceruleus indicates heavily labelled neurons in this region (arrows). Bar in each photograph represents 60 μm.

17, 18, and 19 and the posterior thalamus. The significance of CB's neural connections with apparently non-visual structures (e.g., claustrum, the ventral anterior thalamic nucleus, brain stem nuclei) remains unclear.

A. VISUAL CONNECTIONS–Retrograde studies consistently revealed that lamina III pyramids in areas 17, 18, and 19 project to the CB area (fig. 1E-1K). These data are in substantial agreement with those reported in recent investigations using the less sensitive diaminobenzidene (DAB) modifications of the HRP technique. Maciewicz (1974) reported projections to CB from areas 17, 18, and 19 arising mainly from laminae III cells, with some involvement of cells in deeper cortical laminae, while Gilbert and Kelly (1975) reported that laminae II and III project to CB. Seagraves (1978) studied the connections of the medial (PMLS) division of the lateral suprasylvian area, as defined by Palmer et al. (1978), and also reported heavy input from areas 17, 18, and 19. More recently, Lund et al. (1979) showed with HRP injections that lamina II and III (large pyramidal neurons) of area 17 project to the CB area.

Additionally, morphological support for a possible role of the CB area in visual activities comes from information showing its apparent afferent input from the frontal eye field (FEF) of the cat. Gel placements of HRP into CB resulted in the labelling of neurons in area 6 and 8 ipsilaterally (fig. 1A). The region (area 8) within the presylvian sulcus corresponds to the cat's frontal eye field (FEF) as originally proposed by Scollo-Lavizzari (1964). Area 6 from the ventral lip of the cruciate sulcus to the genual sulcus, is also thought to be a portion of FEF (Schlag and Schlag-Rey 1970) since this area, as well as that within the presylvian sulcus, can produce contralateral conjugate movements of the eyes in the horizontal plane upon electrophysiological stimulation.

Finally, the CB area was also observed to receive its heaviest contralateral projections from lamina III pyramidal neurons of the homologous cortex within the banks and depth of the suprasylvian sulcus (fig. 1H), in agreement with Maciewicz (1974), as well as from a few polymorphic cells of the deeper cortical laminae. Contralateral corticocortical commissural projections were also observed from area 18 and 19.

Subcortical connections of the CB area also provide evidence in support of the proposal that this area plays a role in visual functions. The most notable relationship of the CB area is with the posterior thalamus. The posterior nucleus (PN) and lateral posterior nucleus of this region have been shown to receive direct projections from the superior colliculus (Altman and Carpenter 1961, Berson and Graybiel 1978) as well as from areas 17, 18 and 19

(Graybiel 1972). Such connections are suggestive of visual function.

After a HRP placement in CB, labelled cells were seen throughout the rostrocaudal extent of PN. The results of other studies (Robertson 1976) are in agreement with these findings. In the LP-pulvinar complex (fig. 4A, 4B) labelled neurons were found in the more lateral pulvinar regions dorsal to DLGN and in both the lateral (corticorecipient) and medial (tectorecipient) subdivisions of the lateral posterior nucleus (Berson and Graybiel 1978). These areas would correspond in Updyke's (1977) nomenclature to the pulvinar nucleus and the lateral and interjacent divisions of the lateral posterior nucleus. The observations of Berson and Graybiel (1978) are in partial concurrence with ours having demonstrated that labelled cells appear in the ventral one-half of the corticorecipient zone (posterior nucleus) and the upper two-thirds of the tectorecipient zone after HRP placements within CB.

A consistent pattern of neuronal labelling was found in the central lateral thalamic nucleus (fig. 1E) after HRP placements in CB. A more extensive gel placement revealed labelled neurons in the paracentral and central medial nuclei as well. Several HRP studies (Robertson 1976, Kennedy and Baleydier 1977, Hughes 1978) have suggested a projection from CL to the CB area. Furthermore, since both CB area (Kennedy and Magnin 1977) and internal medullary lamina (Schlag and Schlag-Rey 1971) have been implicated in saccadic eye movements, it would not seem improbable that they could be connected.

Our study also confirmed earlier investigations using degeneration methods (Narikashvili et al. 1969, Niimi and Sprague 1970, Burrows and Hayhow 1971) which indicated the presence of direct projections from the major laminae of the DLGN to CB. In our investigation, the HRP method revealed that the three major laminae (A, AI and C) as well as the medial interlaminar nucleus (MIN) of DLGN project directly to the area of CB (fig. 5A, 5B, 1G). Previous degeneration (Heath and Jones 1971) HRP (Gilbert and Kelly 1975, Robertson 1976, Kennedy and Baleydier 1977) and autoradiographic studies (Rosenquist et al. 1974, LeVay and Gilbert 1976) have suggested that the MIN and/or lamina C of DLGN project to CB but that not all of the major laminae do so. It was believed that the lesions used in silver degeneration studies showing a projection from DLGN to CB actually interrupted fibers of passage in route to CB from more medial thalamic areas (posterior thalamus). However, 2 lines of evidence tend to support the likelihood of a direct geniculo- CB projection. First, in all of our HRP experiments, labelled neurons were seen in the major laminae (fig. 5A, 5B) their number being directly proportional to the size of the injection and/or gel placement. Secondly, the injection site primarily involved the CB area and not other cortical area (17 and 18) known to receive direct thalamic input from DLGN. This was supported by the fact that the most numerous and heavily labelled contralateral neurons were observed in the homologous CB area contralateral to the gel implant site and not in cortical contralateral areas 17 and/or 18. It is felt that since parastriate visual areas (area 18) other than the area 17 receive direct thalamic input from the DLGN (Hollander and Vanegas 1977), it would not seem unreasonable to expect to also find, with more sensitive HRP techniques (Mesulam 1976, 1978), a direct input from DLGN to this extrastriate, visuotopically-organized cortical region.

B. OTHER SUBCORTICAL CONNECTIONS OF CB—The present investigation revealed a substantial claustral–CB projection. This telencephalic derivative is divided into 2 parts (Narkiewicz 1964): a dorsal or insular claustrum and a ventral or prepyriform claustrum. Using retrograde labelling techniques (HRP) a few cells were found containing reaction product within the

dorsal aspect of this nuclear structure. Most of the labelled neurons, however, were found in the intermediate zone between the dorsal and ventral parts of the claustrum. Riche and Lanoir (1978) found the majority of labelled cells in this area of the claustrum following an injection of HRP into the gyrus proreus in the cat. These authors feel that discharge of claustral neurons can occur in conjunction with body, head, or eye movements. In their study, retrogradely-labelled cells were most numerous within the rostral part of the claustrum, while our data revealed a more pronounced labelling in the caudal part. Thus, there may be a rostrocaudal organization within the claustrum since the gyrus proreus is rostral to our injection or gel placement site in the CB area. Finally, Flindt-Egebak and Olson (1978) have shown with autoradiography a projection from the claustrum to the CB area.

It was also demonstrated that the ventral anterior thalamic nucleus projects to the CB area. Multiform cells located primarily in the dorsal and dorso-medial aspect of this thalamic nucleus were labelled following a HRP gel placement in the vicinity of CB (fig. 1D, 3A and 3B). Degeneration (Nauta and Whitlock 1954) and HRP (Mizuno et al. 1975, Robertson, 1977) studies showed a projection from VA to the suprasylvian gyrus of the cat. Mizuno et al. (1975) reported that an injection of HRP into the rostral middle suprasylvian gyrus with involvement of the medial bank of the suprasylvian sulcus coincided with the appearance of HRP-labelled cells in the dorsal and dorso-medial portion of VA. Robertson (1976) has suggested that the thalamocortical projections VA are to the crown of the suprasylvian gyrus and not necessarily to the CB area. Although a portion of the crown was involved in our HRP gel placements and/or injections, most of the site involved the CB area. This concept can be supported again, as in the discussion of the dLGN projections in the CB area on the basis of a much heavier and more numerous labelling of cells in the contralateral CB area. This would be expected only if the main injection site involved its opposite homologue. Also, the labelling of VA neurons was quite substantial–more so than would be anticipated with a slight injection of the crown of the suprasylvian gyrus. Thus, it appears that there is a projection from VA to CB.

The functional significance of the anatomic relationship of VA with the CB area is unclear. This thalamic nucleus has been implicated in the mediation of polysensory evoked responses to the cortex including that on the crown of the suprasylvian gyrus (Robertson and Thompson 1973). These authors suggest that the reticular formation displays polysensory convergence and that this multimodal information can be relayed to cortical association areas by way of the ventral anterior nucleus. In support of our findings, we have also observed a dense reciprocal connection from medial VA to the frontal eye field in the monkey (unpubl.).

The present investigation also demonstrated a projection from various brain stem nuclei to the CB area. Labelled cells were observed in rostral linear nucleus (of Berman), ventral tegmental area (of Tsai), locus ceruleus, and dorsal raphe and superior central nuclei. The ventral tegmental area is thought to be a major source of dopamine, and the locus ceruleus and raphe nuclei of norepinephrine and serotronin respectively. The functional significance of these projections remain an enigma at the present time. The locus ceruleus and raphe nuclei have been found to play important roles in many activities with particular involvement in sleep and wakefulness (Jouvet 1972).

Törk et al. (1979) have also showed using HRP that the above brain stem nuclei project to the visual cortex. Data from their study with either the DAB or paraphenylenediamine reaction showed that the rostral linear nucleus and locus ceruleus nuclei project to each of the three cortical areas (17, 18 and 19), and that the raphe

nuclei (dorsal and superior central) provide input to areas 17 and 18 but not to area 19. Thus, it is not surprising to have observed, with more sensitive methods (Mesulam 1976, 1978), labelled brain stem cells following a HRP placement into the other (CB) area of the cat visual cortex. This evidence is in agreement with generally accepted views of a widespread projection from certain brain stem areas to the neocortex (Bentivoglio et al. 1978).

In summary, the results from the present investigation provide further anatomical support for a possible role of the Clare-Bishop area in visual functions based on the fact that this cortical region has connections with areas distinctly concerned in visual activities such as areas 17, 18 and 19 and the posterior thalamus, including the dorsal lateral geniculate nucleus. The significance of the CB area's relationship with nuclear structures such as the claustrum, ventral anterior nucleus, and certain brain stem nuclei remains unclear at the present time.

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